Attack Mode in a Predatory Gastropod: Labial Spine Length and the Method of Prey Capture in *Acanthina angelica* Oldroyd

by

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Abstract. The function of the labial spine and the feeding behavior of the predatory gastropod *Acanthina angelica* were observed under controlled conditions. Long- and short-spined snails were presented three size classes of barnacle prey. The mode of attack was related to the length of the labial spine and the prey size. The spine was observed to function as a wedge to force apart the opercular valves of the prey (here termed wedging); drilling through the test or valves was an alternative mode of attack. As prey size increased, snails switched from wedging to drilling, with the short-spined snails switching at a smaller prey size than long-spined snails. The long-spined snails consumed medium-sized prey significantly sooner than short-spined snails. Short-spined snails are usually found in association with small barnacles, while long-spined snails predominate among larger barnacles. However, spine length is not fixed, and available evidence indicates that prey size controls spine length.

INTRODUCTION

MANY PREDATORY GASTROPODS attack barnacles, bivalves, and other gastropods by drilling through the shell of the prey (CARRIKER, 1961, 1981). "Wedging" is an alternative mode of attack in several of these species (PAINE, 1962; MACGINITIE & MACGINITIE, 1968); this entails the predator's forcing its shell margin between the valves of the prey (barnacle or bivalve) and, once access is gained, inserting the proboscis to consume the prey. Some members of the neogastropod family Thaididae, which includes the genus *Acanthina,* have apparently taken the wedging approach to attacking prey one step further. These species are characterized by an extension of the shell margin into a labial spine or "tooth."

A variety of functions has been attributed to the spine. HEWATT (1934) and MACGINITIE & MACGINITIE (1968) both observed several species of thaids utilizing the spine as a "pry bar" or wedge to force apart and hold open barnacle valves. PAINE (1966) concluded that the spine of *Acanthina angelica* Oldroyd, 1918, is not used in this fashion, but rather it serves as a brace to afford a firm position on the substrate while drilling. MENGE (1974), working with *Acanthina punctulata* (Sowerby, 1825), arrived at a similar conclusion regarding use of the labial spine. SLEDER (1981), on the other hand, concluded that the spine

of *A. punctulata* helps the predator to apply a fast-acting toxin to its barnacle prey.

Acanthina angelica is endemic to the Gulf of California (KEEN, 1971), and is common in the rocky intertidal of the northern Gulf (TURK, 1981; HOUSTON, 1980). Adult snails attain a total shell length of 35–40 mm, and feed almost exclusively on barnacles (PAINE, 1966). The spine length of adult snails varies considerably among individuals; *e.g.,* 30-mm snails have spines ranging from 2 to 7 mm in length (YENSEN, 1979). The intertidal distributions of the long-spined and short-spined snails are skewed in a manner that reflects the intertidal size distribution of the two dominant barnacle species upon which the snails prey (PAINE, 1966; YENSEN, 1979; TURK, 1981). Long-spined *A. angelica* are more common in the high intertidal zone characterized by the large barnacle *Tetraclita stalactifera* Lamarck, while short-spined snails are usually found in the lower intertidal in association with the small barnacle *Chthamalus anisopoma* Pilsbry. The correspondence between spine length and barnacle size suggests a functional relationship between the two. Both PAINE (1966) and YENSEN (1979) observed that snails with relatively long spines prey on *Tetraclita,* while short-spined snails feed primarily on *Chthamalus.* However, in contrast with Paine's suggestion that the snails only drilled, Yensen's

field observations and laboratory experiments strongly support the hypothesis that the labial spine is used directly in wedging apart the opercular valves of barnacles.

The purpose of this study was to elucidate the relationship between labial spine length, the size of the barnacle prey, and the mode of attack of *Acanthina angelica*. If the spine is used to wedge open the opercular valves of barnacles, and drilling is an alternative to wedging when the spine is too short to effectively reach the valves, then short-spined snails should switch to a drilling mode of attack at a smaller prey size than do long-spined snails. This is assuming that wedging would be quicker than drilling, and that the snails feed in the most efficient manner possible.

MATERIALS AND METHODS

A laboratory experiment was conducted to determine the foraging behavior of both long- and short-spined snails as they fed on three different size classes of barnacles. Specimens of *Acanthina angelica* were collected haphazardly during October of 1983 from the rocky intertidal near Puerto Penasco, Sonora, Mexico (31°18′N, 113°35′W) on the Gulf of California. The animals were brought to the University of Arizona where they were maintained without food in three 40-L aquaria for two weeks. Aquarium water temperature was approximately 22°C, comparable to that in the Gulf during October. Photoperiod was approximately 10 L, 14 D.

Two weeks after the snails were collected, barnacles were collected from the same area. To avoid the potentially confounding effects of using two species of barnacles for prey, as might arise from a species-specific mode of attack, I exclusively collected *Tetraclita stalactifera* over a range of sizes (2–40 mm basal diameter) for presentation as prey. Settlement of *Tetraclita* during the two months previous made it possible to collect adequate numbers of small individuals calculated to be of approximately the same size and body weight as the smaller barnacle species, *Chthamalus anisopoma* (MALUSA, 1983). The barnacles were brought to the University of Arizona and maintained in aquaria next to those harboring the snails.

Forty-five short-spined and 45 long-spined snails were chosen for the experiment on the basis of their spine length. Long-spined snails were defined as those having a labial spine measuring more than 4 mm from base to tip; short-spined snails were defined as those having a spine measuring less than 3.5 mm in length. No attempt was made to control for differences in shell length between the two groups. Long-spined snails were approximately 25–35 mm in length, while short-spined snails were approximately 20–35 mm.

The shells of all snails were numbered with a permanent felt tip marker to permit individual identification. Barnacles were sorted into three size classes based on the basal diameter along the rostral-carinal axis: less than 7 mm (small), 7–20 mm (medium), and greater than 20 mm

(large). Inappropriately sized individuals were removed from the pieces of the substrate bearing barnacles, leaving only the desired size class on each rock.

At the beginning of the experiment, each of the three aquaria received 15 long-spined snails, 15 short-spined snails, and 40 to 60 of one of the three size classes of barnacles. Within each aquarium the two groups of snails were separated by a plastic screen that allowed water passage. Approximately equal numbers of barnacles were made available on either side of the divider. The foraging activities of the snails were then observed continuously for the following 24 h, and thereafter two to three times daily for 26 days. I kept a record of (a) the mode of attack employed by each snail on its first successful feeding (wedging or drilling), and (b) the time from the start of the experiment until the first barnacle was successfully attacked and consumed (here termed the "consumption order"—see below).

The feeding behavior and the use of the spine could be observed closely in instances when the opercular valves of the barnacle were close to the opening of the shell, as is the case in small barnacles and those larger barnacles that happened to have badly eroded tests, permitting an adequate view. Observations of feeding behavior associated with wedging (a characteristic lunging movement described below) allowed me to infer wedging in cases where the snail's foot and mantle obscured direct observation of the spine. In addition, wedging attacks left scratch marks on the barnacle's valves. Drilling attacks could only be identified after the fact by the presence of a hole in the test or valves of the barnacle. I avoided handling the snails while drilling; thus, it was not possible to observe drilling directly. It is not known whether the relative hunger of *Acanthina angelica* modifies its foraging behavior, and consequently after any one snail had consumed a barnacle, both the predator and the remains of its prey were removed from the aquarium.

RESULTS

Close observation of feeding behavior established the following sequence of events. After encountering a barnacle the snail mounted it and brought the labial spine to the barnacle's opercular opening. The spine was then inserted into the opening, as if to "feel" for the opercular valves. The proximate stimulus for a wedging attack appears to be the contact of the spine with the opercular valves. Snails observed wedging kept the spine positioned in or above the opercular opening and, with the foot firmly attached to the barnacle, thrust the spine downward, apparently bringing the spine into forcible contact with the natural separation of the barnacle's opercular valves at a point on the scutum near its junction with the tergum. This "lunging" was repeated as often as five times per minute, until either gaining access to the mantle cavity of the barnacle, or giving up. Some snails maintained an attack for up to several hours, although with diminished frequency of
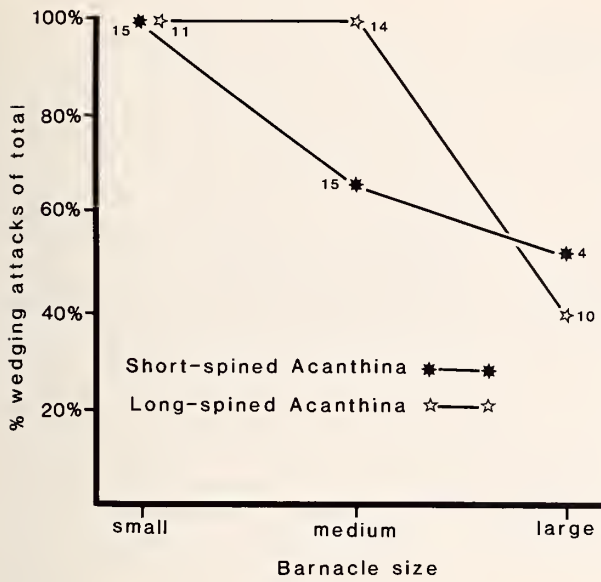
Figure 1

Results of the foraging experiment showing the variation in attack mode in *Acanthina angelica* relative to spine length and size of barnacle prey. Sample size is indicated.

lunging. These prolonged attacks resulted in an abraded elliptical depression where the barnacle's valves meet. This artifact of wedging could be mistaken for a drill hole, except it is not circular (as gastropod drill holes are), and it was associated only with lunging behavior. Interestingly, three snails that did drill failed because they entered the barnacle at a point above the opercular valves, and another snail completed a drill hole into an empty test. Most snails sequestered with the large barnacles either could not feed or chose not to feed during the entire 27 days of observation; these data were not included in the statistical analyses.

Relationships between attack mode, spine length, and the size of prey are shown in Figure 1. These data were analyzed with a G-test (Table 1). The mode of attack is clearly dependent on the barnacle size (G = 20.995, df = 2, $P < 0.001$). One hundred percent of the small barnacles were wedged open with the spine, as were 87% of the medium-sized barnacles, and only 43% of the large barnacles. Hence, successful use of the spine was dependent on barnacle size.

There is also a relationship between attack mode and spine length that varies according to barnacle size. Given small or large barnacles, short-spined and long-spined snails employed similar attack modes (*i.e.*, they both wedged small ones and drilled large ones with similar frequency; $P > 0.50$). However, for medium-sized barnacles, more short-spined snails drilled than did long-spined snails ($0.025 < P < 0.05$) (these tests represent partitioning of the G that is due to the spine length ×

attack mode and the spine length × attack mode × prey size interaction).

Figure 2 shows the time until the first barnacle was consumed for long and short-spined snails on all three size classes of barnacles. Note that this time interval includes the total time from the beginning of the experiment until the first barnacle was consumed, not simply the time from initiation of feeding to completion. Data were analyzed using a Mann-Whitney test for ordinal data by assigning rank values to the observations in each time interval (the "consumption order"). Pairwise comparisons of consumption order show that short-spined snails consumed small barnacles sooner than they did medium-sized barnacles ($P < 0.001$); the medium-sized barnacles were consumed, in turn, sooner than large barnacles ($P < 0.001$). Long-spined snails showed no significant difference in consumption order between small and medium-sized barnacles ($P > 0.20$). Large barnacles did take longer to consume than either small or medium-sized barnacles ($P < 0.001$).

Also using a Mann-Whitney test, I made comparisons between long- and short-spined snails on a given size class of barnacle. The results show no significant difference in consumption order between long- and short-spined snails when feeding on small barnacles ($0.1 > P > 0.05$), but that long-spined snails consumed medium-sized barnacles sooner than did short-spined snails ($P < 0.001$).

DISCUSSION

The results of the feeding experiment support the hypothesis that the labial spine of *Acanthina angelica* functions to force apart the opercular valves of its barnacle prey. Large barnacles were wedged significantly less frequently than either medium-sized or small barnacles, and short-spined snails switched to a drilling attack at a smaller prey size (medium-sized barnacles) than did long-spined snails. These results suggest a close relationship between spine length, barnacle size, and mode of attack.

As noted above, no attempt was made to control for differences in shell length between short- and long-spined

Table 1

Analysis of the relationship between spine length, barnacle size, and mode of attack (G-test, SOKAL & ROHLF, 1969).

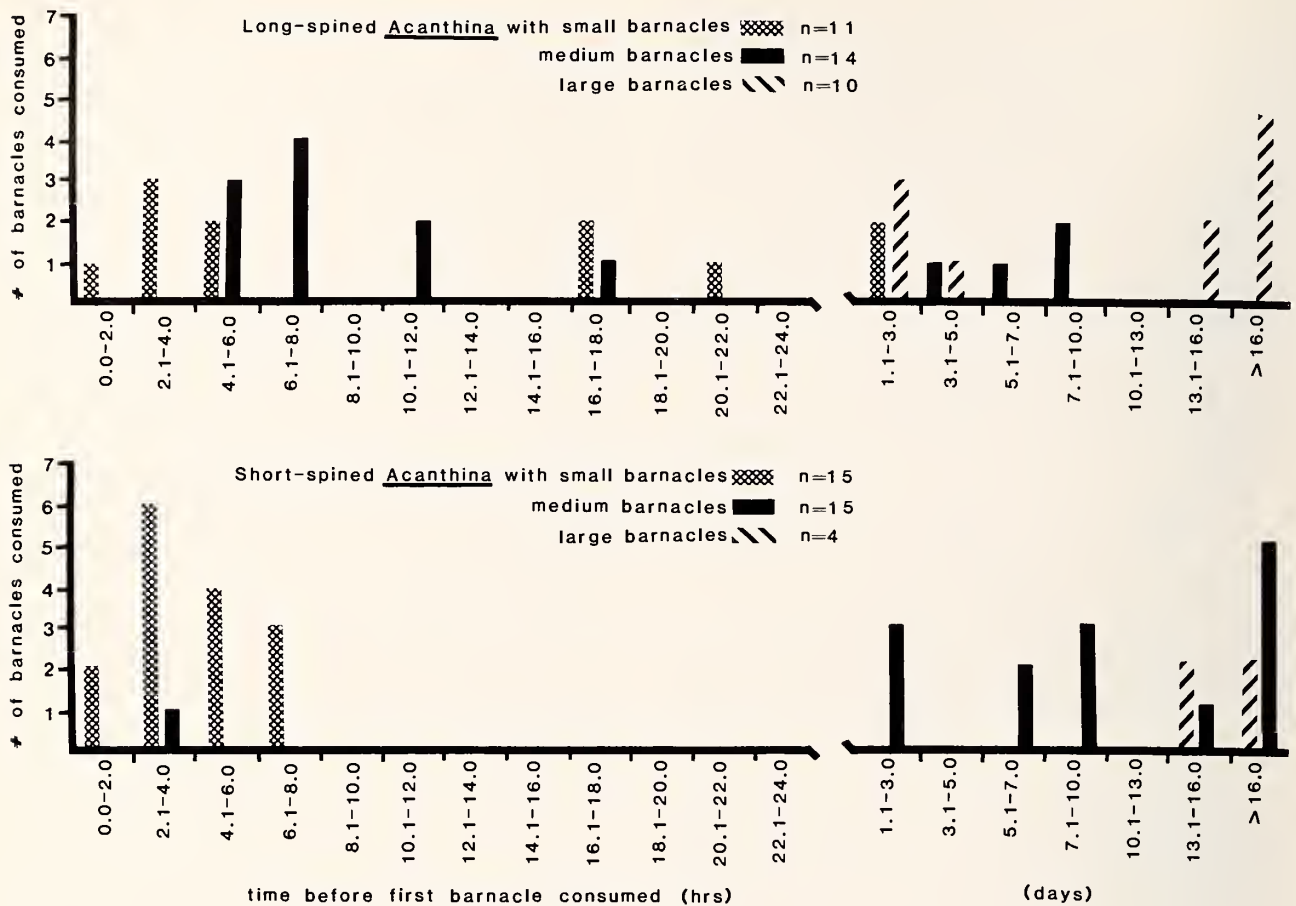| Comparison	df	G
Spine length × barnacle size	2	3.294
Mode of attack × barnacle size	2	20.995*
Spine length × mode of attack (small)	1	0.000
Spine length × mode of attack (medium)	1	7.570**
Spine length × mode of attack (large)	1	0.116
Spine length × mode of attack × barnacle size	7	31.975*

* $P < 0.001$, ** $0.025 < P < 0.05$.

Figure 2

Consumption order of long- and short-spined *Acanthina angelica* feeding on three size classes of barnacles. Time is from the beginning of the experiment until the first barnacle was consumed.

snails used in the experiment. At Puerto Penasco, all *Acanthina angelica* less than 25 mm in length have a short spine (less than 3.5 mm), while larger *A. angelica* may have either a short or long spine (PAINE, 1966; YENSEN, 1979; and personal observations). It is, therefore, likely that in natural populations the mean size of a short-spined snail is less than that of a long-spined snail. The ontogeny of the feeding behavior of *A. angelica* remains to be investigated, but this study suggests that very small snails are probably restricted to drilling.

In general, the drilling of barnacles took considerably longer than wedging. The four failed drilling attempts, the increase in handling time, and the apparent reluctance to drill (judging from the paucity of attacks on the large barnacles during the experiment) indicate that drilling is a relatively inefficient mode of attack in *Acanthina angelica*. Very large barnacles may effectively have a size-escape from predation by *A. angelica*. DAYTON (1971) notes a similar size-escape from predatory thaids by the barnacle *Balanus cariosus* (=*Semibalanus cariosus*).

Two of the barnacles that were successfully consumed

had holes drilled only partially through the test, near the base of the animal; they showed no evidence of other drilling or wedging attacks. PALMER (1982) reports similar incidents in the case of the *Thais* predation on four species of intertidal barnacles from the Pacific Northwest, and suggests (p. 35) that "because *Thais* are equipped with a powerful toxin (HUANG, 1971, 1972), they need only penetrate a barnacle far enough to reach a space that communicates with the rest of the body." Evidence for a toxin that paralyzes prey has also been found in *Acanthina punctulata* (SLEDER, 1981) and *A. spirata* (HEMINGWAY, 1978), indicating that the ability to produce and utilize a fast-acting toxin may be common within the Thaididae. That two incompletely drilled barnacles were nonetheless consumed during this experiment provides circumstantial evidence that *A. angelica* possesses a similar toxin.

The feeding experiment demonstrated that the short-spined snails consumed small barnacles significantly sooner than they consumed either medium-sized or large barnacles. Long-spined snails showed no significant difference in consumption order between small and medium-sized

barnacles. In addition, long-spined snails consumed medium-sized barnacles sooner than did short-spined snails, as might be expected when considering that one-third of the short-spined snails drilled the medium-sized barnacles. There was no significant difference in consumption order between long- and short-spined snails when feeding on small barnacles. This observation raises the question: how do short-spined snails persist in a population where a long spine allows a broader range of potential prey?

YENSEN (1979) found that short-spined snails gained significantly more weight when fed the small barnacle species *Chthamalus* than when fed the large species *Tetraclita* (and the converse for long-spined snails). This suggests that there is some cost, as well as benefit, to having a spine of a particular length. A spine length permitting efficient predation on one size class of barnacle may reduce efficiency on other sizes of barnacle, at least if one considers the extremes of barnacle sizes. In this regard, it is noteworthy that LEVITEN (1976) suggests that the radular tooth of the predatory gastropod *Conus* may be efficient over only a narrow range of prey sizes. A similar trade-off in *Acanthina angelica* would explain the predominance of short-spined snails among *Chthamalus,* and the association of the long-spined snails with *Tetraclita.* However, this experiment was not designed to test the snail's prey preference, as only one prey size was offered to each sample.

Furthermore, the labial spine of *Acanthina angelica* is not fixed in length. YENSEN (1979) has shown experimentally that spine length is controlled by barnacle prey size. Long-spined *A. angelica* offered only small barnacles had significantly shorter spines after three months, while short-spined snails grew longer spines when fed on large barnacles for three months. Controls did not change spine length significantly. Thus, barnacle size is determining labial spine length in a manner that maintains the "proper" relationship between the spine length and the size of the barnacle prey.

ACKNOWLEDGMENTS

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